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THE EMBRYOLOGICAL DEVELOPMENT OF THE SKELETON OF THE HEAD OF BLATTA.[1]

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OUR knowledge of the embryological development of the sclerites of the head of insects is very meager. With but few exceptions the subject has been treated in the most incidental manner and the observations are few and scattered. This is due not only to the fact that attention has been directed to the more general features of insect embryology, but is due also to a lack of systematizing of our knowledge of the structure of the head of the adult insect and to the difficulty of determining the limits of the sclerites before they become firmly chitinized.

Of all the students of insect embryology, Heymons ('95 and '97), Janet ('99), and Comstock and Kochi, (:02), are the ones who have devoted the most attention to this subject and these workers differ radically in their conclusions.

It was in hopes of determining the conditions in one of the more generalized of the pterygote insects that I undertook the study of the embryological development of the skeleton of the

[1]Contribution from the Entomological Laboratory of Cornell University.

head of *Blatta germanica*. This was proposed by Prof. Comstock and to him I am indebted for many suggestions.

In the choice of an object for this study I was guided by the desire to select one of the more generalized forms and one which at the same time would afford an abundance of material. Both of these conditions seemed to be met by *Blatta germanica*. Though undoubtedly highly specialized in some respects, the cockroach is regarded by many students as the most primitive of our pterygote insects. I believe that in this respect one of the Plecoptera would have been more valuable, but as regards abundance of available material it would be difficult to select a form more satisfactory than is Blatta.

On the other hand, as objects of study the embryo of Blatta present certain difficulties which are accentuated in the course of the work. Of these there are "die ausserordentlichen technischen Schwierigkeiten" which Cholodkowsky has so emphasized. These are due primarily to the great mass of yolk, which becomes so brittle as to make it almost impossible to secure complete series of sections by ordinary methods. A more serious difficulty in the work under consideration was the small size of the cells and the indistinctness of the invaginations of the body wall. Of the latter, Wheeler ('89, p. 349) says: "In *Blatta* the formation of the nervous system in its earlier stages cannot be clearly seen from the exterior. The same holds true of the small tracheal invaginations, though several pairs, especially those of the thorax and basal abdominal rings, may be seen on the pluræ in good preparations before revolution. Still they are so much less distinct than in *Doryphora* that I have given them little attention."

THE PRIMITIVE SEGMENTS OF THE HEAD.

The question of the number of segments in the body of the perfect insect early attracted the attention of entomotomists. As the history of the development of our knowledge of the number entering into the structure of the head has been very fully discussed by Comstock and Kochi (:02), I have but little to add to their account.

As early as 1839, Newport discussed this question in considerable detail. He believed in the "correctness of the opinions advanced by Savigny and others, that the organs of manduction are the properly articulated members of distinct segments and are perfectly analogous to the proper organs of locomotion." He attributed the conflict of views to a "too exclusive examination of the head in perfect insects, without reference to the corresponding parts in the larva."

It was thus early realized that it is to the ontogenetic record that we must appeal for a settlement of the question. Unfortunately Newport chose as the basis of his study the larva of *Musca vomitoria*, a form so highly specialized as to be worthless for this purpose. His evidence regarding the possible presence of a fifth segment must therefore be rejected. The value of his conclusion that there were at least four segments was due to his acceptance of the criterion proposed by Savigny.

Zaddach ('54), believed that six segments entered into the composition of the head. Of these the first was the ocular, while the third was the second antennal segment. His evidence regarding the presence of the latter, however, was based upon the erroneous conclusion that in the phryganids the larval antennæ represented the second pair of the Crustacea, and that they were later replaced by the definitive antennæ of the adult, which corresponded to the antennules of the Crustacea.

In 1858 Huxley also discussed the mooted question from the view point of embryology. With characteristic thoroughness and penetration he not only treated of the embryology of an insect, Aphis, but compared its development with that of Crustacea and Arachnida. Granting that the presence of paired appendages was indicative of an equal number of segments, he argues that the absence of the appendages does not necessarily imply the absence of the segment. "No one will pretend that it is so in the abdominal and thoracic regions." In conclusion he proposes the hypothesis "that in the Articulata the head is normally composed of six somites, which are all fully developed only in Podopthalmia, Stomapoda, and some Branchiopoda, while in other Crustacea some one or more of the preoral somites is more or less abortive, and in Arachnida and Insecta the

appendages of the first somite are sessile and those of the second or third undeveloped."

I shall have occasion to revert to this paper of Huxley's, for, as we shall see, he devoted considerable attention to a consideration of the development of the head, and brought out some facts of prime importance.

Packard ('66), believed that the insectean head was composed of seven segments. In 1870, in the second edition of the *Guide to the Study of Insects*, he gives a table of these segments and their appendages. He believed the segments to be a *first ocellary*, *second ocellary*, *opthalmic*, *antennary*, *mandibular*, *first maxillary*, and a *second maxillary* or *labial*. In addition to these seven he includes a hypothetical first segment whose tergal parts give rise to the labrum, epipharynx, and clypeus.[1] Thus at this time he regarded the insectean head as composed of eight primary segments.

In 1871, however, Packard presents evidence to show that the ocelli and the compound eyes do not represent appendages. "Accordingly," he says, "we seem forced to the belief that the head of the hexapodous insect consists of but four segments, *i. e.*, the second maxillary, the first maxillary, and mandibular segments behind the mouth opening and the antennary, or first and preoral segment situated in front of the mouth." This view he reiterates in 1883. In 1898 he tabulates six segments.

One of the most recent workers to approach this subject is Janet ('99). Basing his conclusions largely on a study of the musculature of the adult Vespa, this worker states that the so-called primary head segment — the protocerebral segment of authors — is in reality composed of four segments and that therefore the head of an insect is made up of not less than *nine* segments, all of which were primitively postoral. According to Janet these segments are:

1° Le somite du gésier	ou	somite proto-stomodæal
2° Le somite œsophagien	ou	somite deuto-stomodæal
3° Le somite clypéo-pharyngien	ou	somite trito-stomodæal

[1] "The tergal parts (*i. e.*, the labrum, epipharynx, and clypeus) situated in front of the ocelli, are left out in enumerating the seven segments as they are not supposed by the author to belong to either of those segments." *L. c.* p. 20.

4° Le somite du labre	ou	somite proto-cérébral
5° Le somite antennaire	ou	somite deuto-cérébral
6° Le somite post-antennaire	ou	somite trito-cérébral
7° Le somite mandibulaire	ou	somite proto-gnathal
8° Le somite maxillaire	ou	somite deuto-gnathal
9° Le somite labial	ou	somite trito-gnathal

From the embryological view point Janet sees support for these conclusions in the development of the sympathetic nervous system. He considers "the nervous system of the stomodæum (or the unpaired sympathetic system) as being simply the morphological prolongation on the ectodermic stomodæal invagination, of the chain of the central system." The untenability of this view has been pointed out by Heymons, (:00), who has devoted especial attention to the study of the development of the sympathetic system, and whose argument, therefore, carries especial weight.

Of the work of Patten, Wheeler, Viallanes and Folsom, the excellent résumé by Comstock and Kochi leaves little to be said. These last writers accept Folsom's conclusion as to the presence of seven primitive segments, and agree with him that the appendages of the superlingual segment may be represented in the Orthoptera by a pair of small sclerites lying behind the lingua, within the mouth cavity. Neither Heymons nor Wheeler[1] accept this view. As regards the condition in the cockroach, I have only the negative evidence that there is wholly lacking a trace of a ganglion belonging to this segment. The position of the above mentioned sclerites is such as to make them readily susceptible of explanation on purely mechanical grounds, as secondary structures. Though Folsom's work was done on Anurida, and his corroborative evidence was drawn from a study of other Collembola, it is not to be expected that we should find such a fundamental difference between the Apterygota and the Pterygota.

[1] In a forthcoming paper, which Dr. Wheeler has kindly allowed me to anticipate by the above statement, he very fully and conclusively presents the arguments against such a view.

THE GENERAL FEATURES OF THE FORMATION OF THE HEAD OF BLATTA.

The changes during the first six days [1] of the embryonic life of Blatta lead to the formation of the ventral plate, the blastodermic thickening which represents the first rudiment of the germ band. This extends along about two-thirds of the ventral surface of the egg, beginning at about one-fourth of the length of the egg from its cephalic end.

The newly formed germ band is not an evenly developed structure, but there are to be seen, on each side, groups of rapidly proliferating cells. These active cells give rise to an indistinct segmentation in the earlier stages of the germ band. This was noted by Cholodkowsky ('89), who says, (p. 91): "However, when I say that the young germ band of Blatta gives no indication of cross divisions I do not mean by that that there are no traces of metamerism. Very early when the germ band is still very imperfectly marked off from the surrounding undifferentiated blastoderm, one may observe a noteworthy grouping of its cells around certain points which are none other than the centers for the formation of the future appendages."

Heymons ('95), has correctly interpreted this description of Cholodkowsky's as referring to certain formative centers in the undifferentiated blastoderm, which by their extension and fusion give rise to the germ band. A similar method of formation of the germ band of Astacus had already been pointed out by Reichenbach ('86). That Cholodkowsky was not clear as to the nature of these centers is evident not only from his reference to them as the precursors of the appendages, but also from his Figure 2, which shows an embryo of about ten days, in which the mouth parts and thoracic appendages are already prominent, while there is to be seen "die beginnende Gruppirung der Zellen für die Anlagen des ersten Paares von Abdominalfüssen."

[1] Cholodkowsky ('91), states that on account of the peculiarity of ovoposition, the age of the embryos of Blatta is not easily determined. As an illustration of this, I have found that there may be considerable variation in the degree of development of the embryos of a single capsule. However, the few observations I have made have, in the main, confirmed Wheeler's approximations, and I have followed him in determining the ages of the embryos studied.

An interesting fact is that, as pointed out by Heymons ('95b), the cephalic lobes arise from three pairs of these centers of proliferation, which very early fuse. Wheeler found that two such centers entered into the formation of the lobes of Xiphidium. The presence of the three pairs would preclude Cholodkowsky's idea that these centers represent future appendages. On first thought it might seem that their presence confirms Janet's view as to the compound nature of the preoral region. Janet believes, however, that there are three segments lying cephalad of the cephalic lobes, and that these do not fuse with the lobes, but in the later stages are invaginated with the stomodæum. It is evident that the formative centers of the cephalic lobes lend no support to that view. It has been suggested that they might represent the three segments whose ganglia enter into the formation of the brain. That this is not the case is shown from the fact that these areas precede the definite formation of the germ band, and that their fusion and consequent obliteration has taken place long before the deuto- and tritocerebral segments have united with the protocerebral segment.

It is during the seventh day, after the appearance of the blastoporic thickening of the caudal end, that there becomes prominent a pair of thickenings laterally placed at the cephalic end of the germ band (Fig. 1, *c. l.*). These thickenings represent the cephalic lobes, which are destined to play a most important rôle in the formation of the head capsule. From the first they are connected with the germ band. Of an independent development, such as described by Will ('88) for Aphis and by Heider ('89) for Hydrophilus, I find no indication in Blatta.

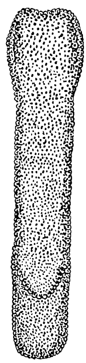

FIG. 1.—The germ band of seventh day. The cephalic lobes (*c. l.*) are indicated. × 120.

During the eighth day of embryonic life the most striking change is the appearance and very rapid development of the amnio-serosal folds,—phenomena which have been described in detail by Wheeler. The cephalic lobes develop rapidly, and during the first half of the ninth day they become prominently demarcated from the strap-like trunk region. The embryo in this stage covers about half of the ventral face of the egg, being somewhat

nearer to the cephalic than to the caudal end. In such an embryo, measuring 1.4 mm. in length, the lobes were .33 mm., about one-fourth of the entire length. Their breadth was .38 mm., compared with .24 mm. for that of the trunk region.

It is during this period that the antennæ appear. These, the earliest of the appendages, are in their origin post-oral. Though generally credited to Weismann, it was Zaddach ('54) who first pointed out this fact. Since that time many workers have confirmed the statement of Zaddach, but more recently it has been seriously questioned. Since the point is one of considerable importance in a determination of the origin of the sclerites, it is necessary to devote especial attention to it in this place.

Viallanes is especially pronounced in his opposition to the interpretation of the antennæ as originally post-oral. In '91, speaking of the 3rd stage in the development of Mantis, he says:

"Les antennes sont encore actuellement les seuls membres en voie de formation, elles apparaissent comme des mamelons à droite et à gauche de la bouche, mais non en arrière de celles-ci. Si au lieu de nous contenter d'examiner un embryon par transparence, nous l'examinons par réflexion, ce qui permet d'en apprécier bien plus exactement le relief, nous constaterons que les mamelons antennaires sont réunis l'un à l'autre par un bourrelet saillant passant en avant de la bouche. Ce bourrelet est fortement incurvé et sa concavité dirigée en arrière embrasse l'orifice buccal. Si nous supposions redressé ce bourrelet aux extrémités duquel se voient les mamelons antennaires, ceux-ci deviendraient nettement prébuccaux. Cette constatation ne nous donne-t-elle pas lieu de penser que les antennes, bien qu'elles apparaissent au niveau de la bouche (c'est-à-dire dans une région du corps qui ne peut être appelée ni prébuccale ni post-buccale), sont réellement prébuccales, bien que déviées de leur situation originelle par suite du développement excessif des lobes procéphaliques?" (p. 288.)

Later, concerning the 5th stage, he says: "Les mamelons antennaires ont grandi; par suite de l'accroissement des lobes procéphaliques ils sont rejetés en arrière et leur situation est devenue nettement post-buccale. C'est l'examen d'états ana-

logues à celui que nous décrivons maintenant qui a décidé la plupart des embryologistes à considérer, à tort croyons-nous, l'antenne comme un membre post-buccal." (p. 289.)

Viallanes was influenced in his interpretation by his studies of the nervous system of the adult, in which the deutocerebrum, the ganglion of the antennal segment, is clearly pre-oral, as is also its commissure.

More recently, Comstock and Kochi (: 02) have challenged the commonly accepted view. Believing that the clypeus "represents the median field of the sternite of the antennal segment," they argue that a study of the figures given by authors describing a post-oral position of these appendages "shows that while a line connecting the two antennæ would pass in some cases behind the mouth it is by no means so clear that the basal part of the rudiment of the antennal sclerite does not abut against the procephalon. In fact, the very figures given to support the view that the antennæ are post-oral in the early embryo support the opposite view." (p. 31.)

A study of Blatta has served to confirm the view of Zaddach. At the time of the first appearance of the antennæ the stomodæal invagination has not yet manifested itself. Its position is marked, however, by an area of rapidly proliferating cells (Fig. 2, *m.*). The antennal rudiments are clearly caudad of this area, and are thus at their earliest appearance post-oral (Fig. 2, *ant.*). They increase rapidly in size, and at a stage but slightly later than that represented in Fig. 2, they lie caudo-laterad of the newly formed stomodæum. It is at this stage that they were studied by Viallanes. Very soon they are pushed more markedly post-orally, and it is in this stage that they have usually been figured (Fig. 3, *ant.*).

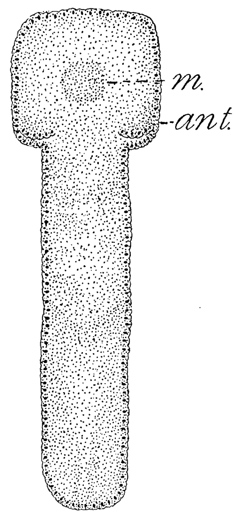

Fig. 2. — The ventral aspect of an embryo of about nine days. The antennæ (*ant.*) have just appeared, while the stomodæum (*m.*) is but indicated by a slight thickening of the cells. × 501.

From the view point of comparative anatomy we have in Apus strong evidence of the original post-oral position of the antennæ.

Lankester thought that in this form the antennæ of the adult were innervated from subœsophageal ganglia. Though this has proven to be incorrect, Pelseneer ('85) has shown that the antennal ganglia of the adult, though associated with, are histologically perfectly distinct from those of the archicerebrum, and that they are perfectly homologous with the ganglia of the ventral cord.

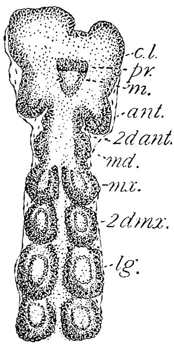

FIG. 3.— Embryo late in the tenth day. The antennæ lie laterad of the stomodæal opening. The procephalon (*pr.*) lies cephalad of the opening. Between the antennæ (*ant.*) and the mandibles (*md.*) lie the second antennæ (*2d ant.*). × 80.

By the end of the ninth day there are to be seen, in addition to the antennal rudiments, those of the thoracic appendages, which are distinctly outlined, while those of the mouth-parts are merely indicated. This is the stage figured by Wheeler ('89, Fig. 44). Wheeler found that in many embryos, as in the one which he figures, "one or, more rarely, both antennary lobes are temporarily bilobed." This he thought might be due to a temporary reversion, 'tending to show that the antennary lobes originally gave rise to two pairs of appendages which were perhaps homologous with the two pairs of antennæ in the Crustacea.' In embryos but slightly more advanced I, also, have seen indications of this bilobulation. Believing that the antennæ of insects are not to be homologized with those of the annelids but, rather, are homodynamous with the other appendages, I should regard this temporarily bilobed condition as a possible reversion toward a biramous condition of the appendage.

The next notable change is the appearance, during the tenth day, of the mouth and of the rudiment of the procephalon. The mouth is not invaginated from within the latter, but, as is shown by Figure 3, lies caudad of it.

There has been much discussion concerning the origin of this rudiment of the procephalon which, by many, is spoken of as merely that of the labrum. A number of observers have reported that in certain forms it originates as a paired structure (Hydrophilus, Kowalevsky, '71, Heider, '89, Graber, '90; *Bombyx mori*, Tichomiroff, '82; Pieris, Gastropacha, Zygæna, Graber,

'90 ; Hyalotoma, Graber, '90 ; Chalicodoma, Carrière, '90, Bürger, '97). Kowalevsky, Patten, Carrière, and others maintain that not only does this structure arise from paired rudiments, but that it represents a fused pair of appendages. Bürger in his edition of Carrière's notes, does not commit himself to the latter view.

On the other hand a greater number of species have been noted in which the procephalon is, from the first, unpaired. Among these are included a number of Apterygota (see Folsom, :00, pp. 93–96), while of the Pterygota may be mentioned Aphis (Huxley, '58) ; Apis (Grassi, '84); Œcanthus (Ayers, '84) ; Forficula (Heymons, '95) ; Mantis (Viallanes, '91) ; Blatta (Cholodkowsky, '90) ; *et al.* Heymons has emphasized the fact that the place of origin of the labrum, *between* the two halves of the nervous system rather than laterad of them, fundamentally distinguishes this structure from the true appendages.

Especial attention was directed to this point in Blatta on account of finding an embryo in which the procephalon was quite clearly in two distinct halves. A study of a large number of other preparations of the same stage failed to duplicate this, though in some there was to be seen a slight mesal constriction. As the embryo first mentioned was otherwise distorted I am inclined to regard the appearance of the procephalon as abnormal, and to agree with Cholodkowsky that in Blatta its rudiment is unpaired.

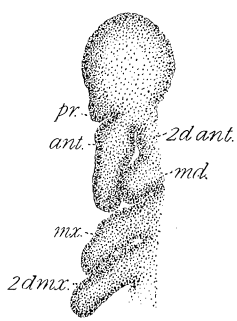

FIG. 4. — Lateral aspect of an embryo a little older than the preceding. × 80.

By the end of the tenth day the embryo has increased considerably in length, and the mouth part appendages are all distinct. In an embryo of 1.5 mm. length, the ocular and antennal segments, which at this time constitute the head of the embryo, measured 275 μ, while the mouth part region was 350 μ in length, their relative extent being thus as 11 : 14. The 1st and 2nd maxillæ are subequal and have relatively the same situation upon the germ band. The mandibles are considerably smaller, but are equally distinct (Fig. 4).

A striking feature of embryos of this period is the relation

of the mandibles to the antennæ. They are separated by a space much greater than that which separates the mandibles from the 1st maxillæ. This appearance, which in Hydrophilus proved so puzzling to Heider, is due to the presence of the so-called "intercalary," "Vorkiefer," "premandibular," or "tritocerebral" segment. As the evidence all tends to show that this segment is the homologue of the second antennal segment of the Crustacea, it should be designated either so or as the *tritocerebral* segment rather than by the indefinite and non-committal term "premandibular."

Wheeler ('93) was the first to demonstrate in Anurida a pair of vestigial appendages, which bear to its ganglion the same relation as do the other appendages to the ganglia of their respective segments. Wheeler's work has been abundantly confirmed by workers on the embryology of the Apterygota, Uzel ('98) and Folsom ('99) having determined that in certain forms these appendages persist even to the adult stage.

Though these results have been generally accepted as applying to the Apterygota, embryologists have been unwilling to accept the scant evidence of the presence of such vestigial appendages in the Pterygota. As long ago as 1870 Bütschli observed in the embryo of Apis a paired rudiment just behind the mouth, which, as he said, "sich fast wie ein Paar innerer Antennen ausnimmt." Bütschli himself did not regard this structure as homologous with the other appendages. Grassi ('84) also noted these appendages, but contrary to Bütschli, who thought that they fused to form a transitory under lip, Grassi states that they quickly disappear without leaving a trace. Moreover, he went farther than Bütschli in comparing them to antennæ, for, as Heider has pointed out, he says, "Il primo paio d'arti boccali, che ha un'esistenza effimera, può forse paragonarsi ad un paio d'antenne degli artrapode" (p. 57). Carrière ('90) described similar rudiments for Chalicodoma, and his statements were verified by Bürger ('97). On the whole, however, insect embryologists discard the above evidence and agree with Heymons ('95 b) who says of the tritocerebral segment, "Sein rudimentär Charakter gibt sich hauptsächlich darin zu erkennen, dass sich an ihm niemals Extremitäten entwickeln. Dies gibt wenigstens, so weit wir bisher wissen, von den pterygoten Insecten."

In the face of these opinions it may seem somewhat venturesome to assert that in Blatta there are evidences of the presence of such appendages. And yet, I believe that the facts warrant this conclusion. In embryos of the eleventh day, in favorable specimens there are to be seen between the antennal and the mandibular rudiments, in the region occupied by the tritocerebral ganglion, small but distinct thickenings of the hypodermis (Fig. 4, *2nd ant.*). Moreover, these are to be detected in both cross and longitudinal sections (Fig. 5), and bear to the ganglion of the tritocerebral segment the same relation which we should expect of appendages. To be sure, not every hypodermal thickening is to be interpreted as the rudiment of an appendage. Since, however, the thickenings under consideration occur not only in one but in several preparations, since they occur in the location we should expect for such appendages and do not occur between the other pairs of appendages, and since, lastly, they bear the expected relation to the ganglia of the second antennal segment, I see no other interpretation than that they represent vestiges of appendages such as are still developed in some of the apterygote insects.

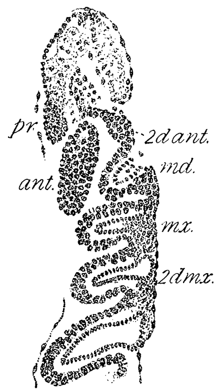

FIG. 5. — Longisection of an embryo of eleven days. × 106.

The mouth-part appendages rapidly increase in size, and early in the eleventh day the length of the 1st maxillæ considerably exceeds that of the second maxillæ, while a little earlier these appendages were subequal. Measuring from the caudal angle to the apex, we find the length of the mandibles to be about 55 μ, that of the 1st maxillæ 96 μ, while the 2nd maxillæ are but 70 μ. There is no trace of lobulation in any of the mouth parts.

The procephalic rudiment has become prominent and, in the latter part of the eleventh day, appears as a button-shaped swelling overlying the mouth. In surface views the mouth can be seen through the rudiment, lying slightly caudad of its center. It is this appearance which has led to the incorrect statement that the mouth develops *in* the procephalon. In embryos of

this age it will be seen that the antennæ are migrating forward. They have increased in length so as to almost completely overlie the mandibles.

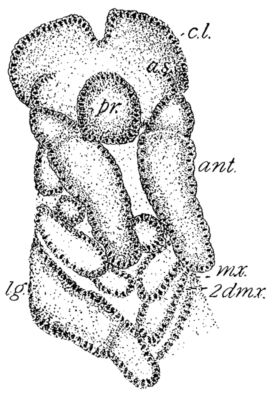

Fig. 6.— Embryo of about thirteen days showing antennal sclerites (*a. s.*) × 80.

The procephalon increases rapidly in size and pushes caudad over the mouth and between the antennæ. In many specimens there is to be noted a constriction of its caudal portion, while the mesal notch of the caudal margin is also distinct.

Early in the twelfth day are to be seen signs of the lobulation of the 1st and 2nd maxillæ. I find no indication of the lobes of these appendages arising from separate, isolated centers, as Heymons ('95a) has described.

It has been stated that the mandibles of Blatta are always simple. I was interested to find that in a few embryos of twelve to thirteen days they appear to be feebly trilobed. This agrees with the condition in Œcanthus, as described by Ayers (p. 24). Korotneff ('81) also represents the mandibles of Gryllotalpa as feebly trilobed (see his Fig. 6), though he says nothing about it in the text.

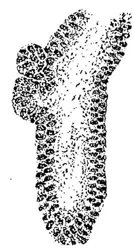

Fig. 7.—2nd maxilla of embryo of about thirteen days, showing lobulation. × 120.

Throughout the series it is evident that there is not a perfect fusion of the antennæ with the cephalic lobes, but the point of origin of these appendages is separated from the lobes by a constriction which demarcates a more or less definite area of attachment for the antennæ. This may be seen in Figure 6.

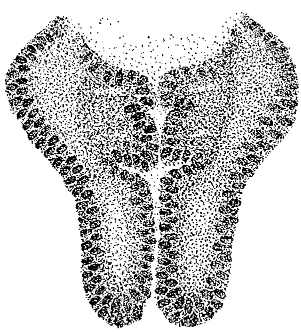

Fig. 8.—2nd maxillæ of an older embryo (about fifteen days) showing the mesad migration. × 120.

The lobulation of the 2nd maxillæ is well shown by Figure 7, which shows one of these appendages from an embryo about thirteen days old. Their mesad migration proceeds rather slowly, until during the fifteenth day they present the appear-

ance shown in Figure 8. They have not yet fused, but the future labrum is clearly outlined. In the meantime they have also migrated forward, so that the space which formerly separated them from the 1st maxillæ has been considerably reduced, and in lateral view the 2nd maxillæ are more or less hidden by the first pair.

About this time there appears a prominent invagination lying cephalo-mesad of the base of the mandible, close to the mandibular ganglion. This lies under the antennæ, but can be seen by focusing below that appendage or by removing it (Fig. 9, *a.t.*). In the same embryos there are prominent ten pairs of tracheal invaginations on the pluræ of the meso-, and metathorax and the first eight abdominal segments. For the prothorax there is a pair of slight and indistinct invaginations which have escaped the attention of previous workers on Blatta. It should be noted that the location of the above mentioned mandibular invaginations is in no wise comparable to that of the tracheæ. In addition to these invaginations there are in the mouth-part region three other pairs — one pair at the cephalo-lateral angle of the mandibles, one between the mandibles and the maxillæ, close to the caudo-lateral angle of the mandibles, and one cephalo-laterad of the base of the 2nd maxillæ. The last pair of invaginations is difficult to detect, for they are smaller, their lumen is not prominent and is frequently hidden by the caudal margin of the 1st maxillæ. It is shown in Figure 10, *p. t.* The invaginations lying laterad of the mandibles form tendons for the mandibular muscles. The rôle of the first and the last pairs in the formation of the tentorium or endoskeleton of the head will be discussed later.

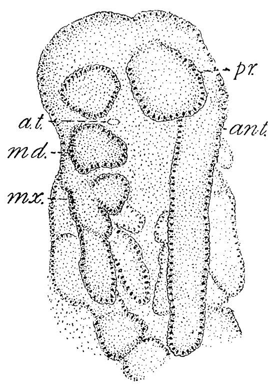

FIG. 9. — Embryo of about fourteen days with right antenna removed, showing the location of the anterior tentorial invagination (*a. t.*) × 80.

Up to this period the length of the mouth-part region has considerably exceeded that of the combined ocular and antennal segments. Thus, as we have seen, in an embryo of about eleven

days the latter region measured 275 μ in length as compared with 350 μ for the mouth-part region. In an embryo at the close of the twelfth day the antennæ have moved forward until the anterior section measures but 200 μ. The mouth-part region, owing to the loss of the tritocerebral segment and the reduction also taking place in the 2nd maxillary segment, measures 280 μ. A comparison early in the fourteenth day shows that the two regions are approximately equal in length. This, as we should suppose from the above, is due not so much to an increase in the size of the anterior region, as to a reduction of the mouth-part region, due to the cephalad migration of the mouth parts. The developing pronotum of the prothorax is pushing rapidly forward, and is limiting the pleural region of the maxillary segments (Fig. 10, *pn.*).

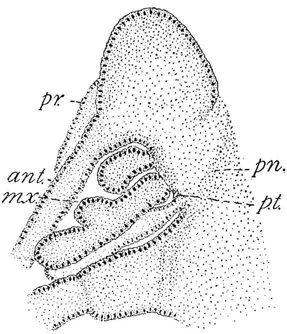

FIG. 10. — Embryo of about sixteen days, showing posterior tentorial invagination (*p. t.*) and the reduction of the mouthpart region. The pronotum (*pr.*) has pushed forward until its anterior margin lies over the first maxilla. × 53.

During the sixteenth day there occurs the series of changes which Wheeler ('89) has described as the revolution of the embryo. This is a period of very rapid growth, and at its close there has been completed the circumcrescence of the yolk by the embryo.

At about the beginning of the sixteenth day, just as these changes have commenced, the conditions do not differ markedly from what I have just described.

The reduction of the mouth-part region is rapidly progressing, the length of the anterior measuring 200 μ as compared with 160 μ for the mouth-part region. The pleural region of the prothorax has extended forward until its most cephalic point lies over the base of the 1st maxillæ, while its indistinct spiracular invagination lies over the base of the 2nd maxilla. The cephalic lobes have extended back until they lie well over the base of the mandibles. The 1st maxillæ greatly exceed the 2nd, which have all but fused to form the labium.

In ventral view of embryos about this age the appendages completely hide the sternal region; but on carefully dissecting

away the antennæ and the procephalon, it may be seen that the sternites of the mandibular and 1st maxillary segments have fused, and form a well marked area lying between their respective appendages (Fig. 12, *hyp.*). We shall refer to this again, in the discussion of the development of the sclerites.

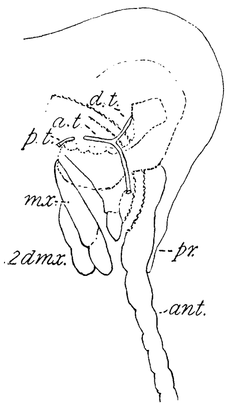

Fig. 11. — Diagram showing the arms to the tentorium in their relation to the nervous system and mouth parts.

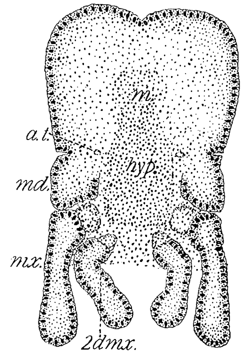

Fig. 12.—Ventral view of embryo of sixteen days. The antennæ and the procephalon have been removed to expose the hypopharynx. × 80.

The procephalon is much enlarged and at its proximal end is wedged in between the cephalic lobes in the manner described by Huxley ('58).

The change which Weismann described as a rotation of the cephalic lobes as upon an axis, occurs during the latter part of the sixteenth and the early part of the seventeenth days. This change is best followed by observing the relations of the brain lobes and of the tendon invaginations to the rest of the cephalic region. At its close the cephalic lobes have pushed over the mandibles in such a way as to crowd back the mandibular pleurites. The mouth parts assume much their definitive position, and the head is practically formed, though it is not until much later that the sclerites have become so chitinized as to be perfectly distinct.

The Development of the Tentorium.

The tentorium or internal skeleton of the head of the adult cockroach has been described and figured by Miall and Denny ('86) and, more fully, by Comstock and Kochi (:02). The latter have treated of its structure in a number of forms, and have shown that its attachments afford valuable criteria for homologizing sclerites in different insects.

In the adult Blatta the body of the tentorium consists of a

chitinous plate underlying the œsophagus and protecting the sub-œsophageal ganglion. From the anterior margin of the body of the tentorium there extends forward a pair of processes, the *anterior arms*, which are attached at the cephalo-lateral angles of the clypeus, near the bases of the mandibles. Corresponding with these are the *posterior arms*, which are near the margin of the occipital foramen, just above the articulation of the maxillæ. In addition there passes up from the body of the tentorium to be inserted at the margins of the antennal sclerites, a third pair of processes, the *dorsal arms*. The entire structure arises from two pairs of ectodermal invaginations.

As early as the thirteenth day there appears cephalo-mesad of the base of the mandibles a prominent pair of invaginations which give rise to the anterior arms (Fig. 9, *a. t.*). These invaginations lie close to the latero-anterior angles of the mandibular ganglion. Heymons refers to the anterior arms in Forficula as originating at the base of the antennæ. In Blatta they are hidden by the antennæ, which must be removed in order to see the invaginations distinctly; but they clearly belong to the mandibular segment.

The invaginations for the posterior arms lie cephalo-laterad of the bases of the 2nd maxillæ (Fig. 10, *p. t.*) They are much less prominent than those of the anterior arms, and, more or less hidden by the 1st maxillæ, they are difficult to detect. They seem to be somewhat retarded in their development, for I have been unable to find them in embryos which clearly showed the invaginations in the mandibular segment.

The invaginations of the anterior arms extend upwards along the sides of the mandibular ganglion, and then, bending at an angle, pass caudo-mesad. At a comparatively late date the two invaginations fuse, and thus give rise to the main body of the tentorium. On the other hand the posterior invaginations pass as blind sacs slightly upward and then forward, to fuse ultimately with the anterior arms.

While the anterior and the posterior arms thus originate as invaginations of the body-wall, the dorsal arms arise, not as invaginations but as processes, from the anterior arms. These processes gradually extend dorsad and thus come into connec-

tion with the body-wall in the region of the antennal sclerites. Figure 11 shows diagrammatically the course of the tentorial arms in an embryo of about eighteen days.

Considering the rapid growth of the embryo during the period following their appearance, the development of these rudiments is but slow. It is not until the twentieth day or later that the fusion of the two pairs of rudiments has taken place.

In view of this method of origin of the dorsal arms of the tentorium of Blatta, it is interesting to note the condition in the Plecoptera, a group in many respects more generalized than the Blattidæ. Of the dorsal arms in these forms Comstock and Kochi, p. 41, say: "In the Plecoptera it appears to be merely a chitinized tendon, the peripheral end of which is less chitinized than the base and is only loosely attached to the skull." Believing that in other insects the anterior arms arise from a distinct invagination, these authors continue: "It remains to be determined whether or not the dorsal arms in the Plecoptera are homologous with the apodeme-like dorsal arms in other insects and, if so, which type is the more generalized." As has been seen, the evidence of embryology shows that the generalized condition is that which still persists in the Plecoptera.

The most thorough study of the development of the tentorium was that of Heider ('89). In addition to this investigator, several others have devoted more or less attention to the subject. Hatschek ('77) called attention to what he supposed were tracheal invaginations in the head of lepidopterous embryos. Tichomiroff ('79) says: "There exists no head tracheæ such as Hatschek thought he discovered. The epithelial invaginations here found I believe to be the rudiments of the inner head-skeleton." Ayers ('84) noticed invaginations in the head region, but was unable to determine their rôle. He inclined to the belief that they disappear altogether, "as no trace of them was to be found in sections of an embryo about the time of hatching." Wheeler ('89) attributed the tentorium to five pairs of invaginations anterior to the maxillary segment.

My results agree with those of Heider, who described the tentorium as arising from two pairs of invaginations, one in the

mandibular and one in the second maxillary segments. Heymons ('95) basing his conclusions mainly on a study of Forficula, described essentially the same conditions, as applying to Forficula and to the Orthoptera, including the Blattidæ. Carrière and Bürger made the same observations on Chalicodoma, thus lending strength to Heymon's surmise that such a mode of origin is typical for the entire group of insects.

Various investigators, among whom are Palmen ('77), Hatschek ('77), Wheeler ('89), and especially Carrière ('90), and Bürger ('97), have regarded the tentorial invaginations as homodynamous with the tracheal invaginations. To this Korschelt and Heider ('93) object that their rudiments do not by any means everywhere agree so closely with tracheal stigmata of the following segments as they do in Chalicodoma. This is especially true of these rudiments in Blatta. As we have seen, the invaginations for the anterior arms arise close to the median line, just laterad of the nerve cord. This corresponds more nearly to the position of the invaginations for the thoracic furca. The origin of the posterior invaginations is more suggestive of the stigmatic invaginations.

In considering this question it must be remembered that Chalicodoma is a highly specialized type with an interpolated larval stage, while Blatta is a representative of a comparatively generalized group of hemimetabolous insects. This being the case, it does not seem that we should regard the location of the tentorial rudiments in Chalicodoma as primitive, but rather I should regard it as secondary. The fact urged by Palman, that the chitinous lining of the tentorium, like that of the tracheæ, is shed during ecdysis, is of little weight, since the same holds true of any hollow ectodermal invagination in insects.

However, it is not necessary to conclude that the tentorial invaginations are metamorphosed tracheæ "which have lost their primitive function and become secondarily modified." If, with Kennel, we derive the tracheæ from dermal glands of annelidan ancestors, there is no reason why we should not consider the tracheæ and the tentorium as homologous structures. Certain of these glands definitely localized have become modified to form tracheæ, while certain others, of the same origin though not

homodynamous with the first, have become converted into the tentorium.

The Development of the Head Sclerites.

As before stated, it is only in the most incidental manner that insect embryologists have touched upon the development of the head sclerites. Before presenting my conclusions concerning the development of the head capsule of Blatta, I shall briefly review the more important of the scattered references, reserving comment until we are ready to compare the views thus expressed with the results of my work.

The earliest of the references was that of Zaddach ('54). This pioneer worker has not received due credit for what he so independently accomplished. Many general features of the embryological development of insects, though credited to much later writers, were clearly outlined by Zaddach. Working altogether with entire mounts, it is but natural that his conclusions regarding the external changes should be the most accurate. It was he who first pointed out the post-oral origin of the antennæ, and called attention to a special antennal segment distinct from the cephalic lobes. He described the procephalon ("*Vorderkopf*"), and derived from it the labrum, the clypeus and the front ("*hinterer und vorderer Kopfschild und Oberlippe*"). He believed that the cephalic lobes formed the bulk of the head capsule, while the Y-shaped suture represented the line of fusion of the cephalic lobes and the procephalon.

Huxley ('58) gave a more accurate description of the procephalon. He also gave a fuller account of the dorsal flexure of the cephalic region, as a consequence of which "the line of attachment of the bases of the eyes and antennæ is frequently altogether above that of the other appendages, so that they appear to be tergal, and not sternal, appendages." The procephalic lobes he regarded as the sternite of the first, or opthalmic, segment and though he does not make a direct statement, the inference is that his "antennulary and antennary sterna" are represented by the labrum and the clypeus.

Packard in his earlier work devoted some attention to the

study of the development of the head sclerites. In 1866 he argued that "since the arthropleural is the limb-bearing region of the thorax it must follow that this region is largely developed in the head," the sternites being reduced to a minimum and the tergites almost completely absorbed. He believed that the bulk of the head is formed "by the great expansions of the eye-pleurites which, so to speak, are drawn back like a hood over the basal rings."

In 1870, in the second edition of his "Guide to the Study of Insects (foot-note)," he reiterates these conclusions. He distinguishes the labrum, epipharynx, and clypeus as tergal elements belonging to his hypothetical pre-ocellary segment. The occiput also is reckoned with the tergites, while the gula is sternal. All of the other elements of the capsule are supposed to be pleural.

Packard later completely revised his views as to the number of primitive head segments. Instead of seven or a possible eight, he recognized but four segments entering into the formation of this region. In 1883, in his paper on "The Number of Segments in the Head of Winged Insects," he thus summarizes his views as to the development of the sclerites:

"It appears, then, that the epicranium or that piece (sclerite) bearing the eyes, ocelli, and antennæ, and in front of the clypeus and labrum, is formed from the original procephalic lobes, and represents the first or antennal segment; while the remainder of the original or primitive segments are obsolete, except in those insects which retain traces of an occiput or fourth cephalic tergite. All of the gular region of the head probably represents the base of the primitive second maxillæ."

Ayers ('83) refers to the reduction of the maxillary and mandibular segments, "their dorsal portions disappearing altogether and their ventral portions fusing with the oral region."

Viallanes ('86 and '87b) states that the head of an insect presents three prebuccal segments and that the labrum represents the sternite of the third or tritocerebral segment. Beyond this he does not enter upon a discussion of the origin of the sclerites.

Heider ('89) was the first to devote especial attention to the development of the tentorium. His careful studies of the origin

of this structure have already been discussed. Regarding the sclerites he states that the labrum and the clypeus arise from the procephalon, while the remainder of the head capsule is formed mainly by the bending over dorsally and the backward extension of the cephalic lobes.

It is Heymons who has devoted the most attention to a study of the embryological development of the head sclerites. Studying mainly the development of various species of the Orthoptera, he very definitely stated his conclusions in his paper on the segmentation of the insect body ('95a). The labrum and the clypeus he derives from the procephalon, while the front, he concludes, is developed from the fused cephalic lobes. The vertex, occiput and genæ he believes are developed from the fused tergites of the mouth part segments, while the hypopharynx arises from the fusion of the sternites of these same three segments.

Janet, '99, finds in the sclerites but little indication of the primitive segments. Thus he finds that the front "appartient, par sa partie antérieure, au somite clypéopharyngien; par sa partie postérieure, au somite du labre; par ses parties latérales, au somite antennaire." Based upon years of study of the morphology of certain Hymenoptera, Janet's paper presents a fund of valuable anatomical data. From the embryological view point it is less satisfactory. Moreover, though recognizing the confusion in the use of terms to designate the head sclerites, Janet has made no attempt to determine homologies. Until this has been carefully done, results obtained from a study of such a group as the Formicoidea can be of but little general application.

On the other hand, Comstock and Kochi, :02, attach very great importance to the relation of the primary segmentation to the sclerites of the adult insect. Their conclusions were based upon comparative anatomical studies of a large series of the more generalized insects, as well as upon embryological data. According to their view, the typical segment is composed of two subsegments. Ventrally the line of union of these subsegments is determined by the position of the furcæ, while laterally it is similarly marked by the position of the lateral apodemes. Between the segments lie the tracheal invaginations, which these

authors regard as homodynamous with the invaginations of the lateral apodemes. Thus to these invaginations of the body wall is ascribed a prime importance in determining the homologies of the sclerites. Another valuable criterion they found in the relations of the appendages to a typical segment.

In addition to limiting and carefully defining the sclerites already generally recognized, Comstock and Kochi also distinguished four pairs of sclerites which had previously escaped attention. These were: 1st, the antennal sclerites bearing the antennæ; 2nd, the antecoxal pieces of the mandibles, a pair of sclerites in some species distinct from the clypeus and forming the ventral articulations of the mandibles; 3rd and 4th, two pairs of maxillary pleurites, narrow, chitinized bands between which articulate the cardines of the maxillæ. In addition to these four pairs of sclerites proper, there are two pairs which may have originally represented segments of appendages. These are: 1st, the ocular sclerites, a pair of annular sclerites bearing the compound eyes, and 2nd, the trochantins of the mandibles, a pair of sclerites between the mandibles and the genæ.

Their conclusions regarding the relations of the head sclerites to the primitive segments and to the appendages were summarized by Comstock and Kochi in the following table:

SEGMENTS	SCLERITES	APPENDAGES
1. Ocular (Protocerebral)	vertex and genæ .... front	Ocular sclerites
2. Antennal (Deutocerebral)	Antennal sclerites .... Clypeus proper	Antennæ
3. 2nd Antennal (Tritocerebral)	Labrum (mouth)	2nd Antennæ of Campodea et al
4. Mandibular	Postgenae. .... Antecoxal pieces Pharyngral sclerites	Mandibles Trochantin

5. Superlingual		Superlingual
6. Maxillary	Maxillary pleurites Lingua	Maxillæ
7. Labial	Lateral cervical sclerites Dorsal cervical sclerites Vent. cerv. scl. (gula)	Labium

In each section of the middle column the dotted line indicates the division between the sternal and the lateral elements of the segment.

My results have convinced me that so intimate a relation between primary segmentation and the sclerites cannot be shown.

I find that the front, clypeus, and the labrum are all derived from the procephalon. This is in agreement with the conclusion of Zaddach, '54, whose "hinterer Kopfschild" is clearly the *clypeus posterior* of Newport or the *front* as defined by Comstock and Kochi.

Aside from Zaddach practically all authors agree in stating that from the procephalon arise the clypeus and the labrum. It has been suggested by Comstock and Kochi that the term *clypeus* has thus been used in a broad sense to include both the clypeus anterior and the clypeus posterior or the front.

That Heider used the word clypeus in a yet looser sense is evident. He speaks of the procephalon as giving rise to the clypeus and the labrum. Now, in Hydrophilus, the form upon which he worked, as well as in any of the Hydrophili, the larva does not possess a labrum (Schiodte, '61), or, more correctly speaking, the clypeus and labrum have fused without leaving any line of demarcation between them. Thus Heider has homologized the clypeo-labral sclerite as labrum only, while the front he has mistaken for the entire clypeus.

On the other hand, Heymons, as is shown by his figures, has correctly distinguished the front. Yet he states that the clypeus and labrum arise from the procephalon, while the front is formed from the fused cephalic lobes. He presents no evi-

dence, nor have I been able to find any in support of this view. There remains a consideration of the relation of these sclerites to the primitive segmentation. I have called attention to the fact that though Huxley, '58, does not make any definite statement to that effect, the inference is strong that he regarded these sclerites as representing the sternites of three preoral segments. In fact, in referring to the Crustacea, he says that the labrum represents the sternite of the antennary or third somite. Viallanes, who likewise refers the labrum to the sternite of his tritocerebral or third somite, seems to have attributed to these sclerites a similar definite relation to the primary segmentation.

More recently Comstock and Kochi have independently arrived at and very definitely present the view that the front, clypeus, and labrum represent respectively the sternites of the first three segments. In support of this view they lay much weight on Viallane's statement that the labrum is innervated by the tritocerebrum. Since the front bears one or more of the ocelli, it is obviously derived from the first or ocular segment. The intermediate sclerite, or clypeus, would then belong to the second segment. These writers also believe that the position of the antennal rudiments is only apparently post-oral, — that in reality the basal part of the antennal sclerites abuts against the procephalon.

The embryological evidence, however, shows that the procephalon, and thus the sclerites derived from it, — the front, the clypeus and the labrum, — belong to a single segment, the ocular or protocerebral.

I have discussed elsewhere the question of the primitive position of the antennæ, and have shown that in Blatta their rudiments are clearly post-oral at first.

Even if we were to grant that the antennal rudiments are only apparently post-oral, there can be no question as to the primitive location of the second antennæ and the third somite. Yet the hypothesis derives the labrum from the sternite of this segment.

While I should attach great value to the innervation as a criterion for determining the relation of sclerites to segments, I

do not believe that it can be regarded as absolute. At any rate, the evidence against the labrum as the sternite of the third segment completely outweighs this consideration.[1]

The procephalon develops entirely in front of the stomodæal invagination, and is already well outlined before the deutocerebral and tritocerebral ganglia have moved forward. Moreover, as Prof. Comstock suggested, the labrum and the clypeus give no satisfactory evidence of a paired origin. The absence of median sutures in these sclerites might be readily explained by the statement that fusion had taken place at such an early stage as to be complete. But a more serious objection is that if they develop post-orally and migrate to their pre-oral position, there should be a stage in which they are paired. Such a stage does not occur.

In the Orthoptera and in the Pterygota generally, the second antennal segment is so slightly developed and so transient as to have been largely overlooked by investigators, yet in these forms the labrum is usually strongly developed. On the other hand, in the Apterygota, where the second antennal segment is especially well developed, the labrum is comparatively insignificant.

Finally, the sutures separating the front, clypeus, and labrum are developed at a comparatively late period in the development of the procephalon. If these sclerites represented primary segments, we should find them developing from three distinct centers. The fact that the procephalon develops as a single piece shows that the sclerites derived from it are not primary, but are secondarily developed. In fact, they are not constant, but there are many species in which one or more of the sutures is lacking, and thus the number of sclerites reduced.

The vertex, the compound eyes, and with them the ocular sclerites and the genæ, are formed from the fused cephalic lobes and thus, with the front, clypeus and labrum, belong to the ocular or protocerebral segment. The median suture of the epicranium represents the ventral line of fusion of these lobes.

[1] It should be noted that Janet ('99) considers the labral nerves as in reality arising from the protocerebrum. This is more in harmony with the embryological evidence.

The V-shaped epicranial suture in Blatta separates the front from the vertex. It thus represents the line of separation between the cephalic lobes and the procephalon.

Heymons maintains that the front alone is derived from the fused cephalic lobes. The relatively excessive development of these lobes would indicate that they must enter more largely into the structure of the head. More weighty evidence is the fact that the front is separated from the compound eyes by the V-shaped suture. There is, of course, no question that the eyes belong to the first segment and are developed from the cephalic lobes. Moreover, in following through a series of embryos we can trace the manner in which the front develops by the extension of the procephalon into the angle between the fusing lobes. Thus the direction of this suture — an inverted V with the apex continuous with the median suture of the epicranium — is easily explained. Heymons emphasizes his belief that the suture represents the line of separation between the first and second segments. But if that were the case the rounded caudal margins of the cephalic lobes would on fusing present a V-shaped angle whose apex would be directed cephalad rather than caudad, as is really the case.

On first sight it would seem obvious that the genæ belonged to the mandibular segment. Huxley ('78) described the mandibles as articulating with this sclerite. To this, Miall and Denny ('86) take exception. Comstock and Kochi also call attention to the fact that the chief articulation of the mandibles is with the postgenæ rather than with the genæ. In the earlier stages, after the mandibles have moved forward, it appears as though the mandibular pleurites occupied the position of the future genæ. At the time of the rotation of the embryo, however, the cephalic lobes crowd forward over the dorsal end of the mandibular segment, and thus the pleurites are pushed back to occupy the position of the postgenæ.

It is easy to see how, as a result of this process of displacement of the mandibular segment, there should remain a portion to serve as the ventral articulation of the mandible. In the adult Blatta the limits of this remnant are not to be distinguished from the clypeus; but, as pointed out by Comstock and

Kochi, in Gryllus and in Corydalis there persists a definite sclerite. These authors have shown that this sclerite bears the same relation to the articulation of the mandible as does the antecoxal piece to the coxa of a thoracic leg, and they have therefore called it the *antecoxal piece* of the mandible.

Along the caudal margin of the postgenæ, but cephalad of the invagination for the posterior arm of the tentorium, is a narrow sclerite, which was first pointed out by Comstock and Kochi. Believing that the posterior tentorial invagination belonged to the first maxillary segment and was homodynamous with the invaginations of the thoracic lateral apodemes, these writers named this sclerite the *anterior maxillary pleurite*. A similar narrow sclerite lying parallel with the first, but caudad of the tentorial invagination, they called the *posterior maxillary pleurite*. We have seen that the posterior arm of the tentorium belongs to the labial segment. The position of its opening in the adult insect — almost directly over the cardo of the first maxilla — is due to the cephalo-mesal growth of the paired labial rudiment, as well as to the backward pushing of the maxillæ at the time of rotation. Thus the sclerite lying caudad of this opening belongs, not to the maxillary but to the labial segment, and should be known as the *labial pleurite*. The sclerite lying cephalad of the opening may retain the name of maxillary pleurite.

However, we cannot restrict the maxillary pleurite entirely to this narrow sclerite. There early takes place a fusion of the pleurites of the mouth part region. The position of the posterior tentorial invaginations serves to mark the anterior limits of the labial pleurite, but the extent of the mandibular and the maxillary pleurites can only be judged from the relations of their appendages. In an embryo of about the sixteenth day, as may be seen from Figure 10, the maxillary pleurites exceed in size either of the others. Though the rotation of the embryo results in a displacement of the maxillæ, I do not believe that their pleurites become reduced to the narrow, imperfectly demarcated sclerites which have been designated as the maxillary pleurites.

We have seen that a portion of the deutocerebral segment, bearing the antennæ, is more or less clearly marked off from the remainder of the germ band, even in the earlier stages. I

believe that this persists as the antennal sclerite of Comstock and Kochi. In embryos about ready to emerge these annular sclerites are very clearly marked, and allow of no question as to their equivalence to other sclerites.

There has been much discussion as to the origin and significance of the hypopharynx, though the data have been drawn almost solely from a study of comparative anatomy. Apparently the majority of those who have thus studied it regard it as representing a fused pair of appendages. Vayssiere ('82) who worked upon larval Ephemeridæ, strongly favored this view, though he adds that in order to settle the question studies of a number of representatives of the various orders would be necessary.

Folsom (:00) derives the hypopharynx of Anurida from a median unpaired evagination between the first maxillæ, and two small papillæ between the mandibles. The first gives rise to the lingua, while from the latter are developed the superlinguæ. The superlinguæ Folsom regards as the appendages of a distinct segment, provided with a small ganglion. He brings forward much evidence from comparative anatomy to show that the hypopharynx of Anurida is typical of the Apterygota. Further than that, he attempts to apply the same interpretation to the Pterygota.

The only worker who has devoted any attention to the embryological development of the hypopharynx of the Ptergota is Heymons ('95a). This investigator reached the surprising conclusion that the hypopharynx represents the fused sternites of the mouth part segments. That this interpretation is essentially correct my studies have convinced me. However, I would not attribute to the labial sternite any part in this structure. I believe that the hypopharynx of Blatta represents the fused sternites of the mandibular and first maxillary segments (Fig. 12, *hyp.*), and that of a consequence of the forward migration of the mouth parts these fused sternites have been pushed to within the mouth cavity.

In Blatta, then, the sternite of the labial segment is represented only by the ventral cervical sclerites. It seems to me very clear that Comstock and Kochi are right in regarding the gula of Coleoptera and certain other insects as representing the fused cervical sclerites.

My views in regard to the relations of the sclerites of the adult Blatta to the primitive segments may be summed up in the following table:

SEGMENT	SCLERITES
Protocerebral	Vertex, genæ. Front, clypeus and labrum.
Deutocerebral	Antennal sclerites
Tritocerebral	———
Mandibular	Part of post-genæ, trochantins Part of hypopharynx
Maxillary	Remainder of post-genæ, maxillary pleurites Remainder of hypopharynx
Labial	Labial pleurites; lateral cervical sclerites Ventral cervical sclerites

From the above results it would seem that the definitive sclerites can afford us little or no evidence as to the primary segmentation of the insects. This is certainly true of the head sclerites, and I see no reason why it should not apply to other regions of the body. Sclerites originate from mechanical causes, and do not necessarily have any relation to the primary segmentation.

As an illustration might be cited the breaking up of the annular segment into sternite, pleurites and tergite. The circumcrescence of yolk and the consequent formation of the lateral and dorsal portions of the embryo is a process of gradual growth, and there is no demarcation into separate areas. The distinction into sternite, pleurites, and tergite is a secondary process.

More germane is the fact of the origin of the front, clypeus, and labrum from the procephalon. Thus not only these three sclerites but also the vertex and the genæ arise from the one segment, the protocerebral. I have shown, also, that the post-genæ are to be regarded, not as the pleurites of a single segment, but as the fused pleurites of the mandibular and maxillary segments.

I would not depreciate the value of the sclerites as an index to relationship among insects. That they are to a marked

degree constant, and that they may be homologized in the different groups, I believe to be very true. That they are secondary is equally true, and thus evidence drawn from a study of the sclerites of the adult insect is insufficient to determine the primitive segmentation and the related question as to the compound nature of the segments.

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